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Hidetoshi Ota

Tropical Biosphere Research Center
University of the Ryukyus
Okinawa, Japan

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Island colonization by *Lipinia noctua* (Reptilia: Scincidae) in Melanesia: Molecular phylogeny and population structure based on mitochondrial *cytochrome b* and 12S rRNA genes

Christopher C. Austin

Evolutionary Biology Unit, South Australian Museum, Adelaide, South Australia, 5000 Australia

Abstract

A molecular phylogenetic analysis of five populations of the scincid lizard *Lipinia noctua* from Melanesia is presented based on DNA sequence variation from a total of 693 aligned sites from the mitochondrial *cytochrome b* and 12S rRNA genes. The two datasets show general congruence, but the placement of one population from the north coast of New Ireland Island (Kavieng) are incongruent. The Kavieng population groups with high bootstrap support with the New Guinea populations for the *cytochrome b* dataset, but with the highland population from the Lelet Plateau, New Ireland, for the 12S rRNA dataset. Estimates of the transition/transversion bias based on maximum likelihood reduce the heterogeneity and in the combined dataset the former grouping is supported with a low level of bootstrap support. Genetic distances demonstrate large population structure in *L. noctua* from the Melanesian region which is in contrast to previous work on morphology that showed little or no variation among Melanesian populations. The Lelet Plateau of New Ireland Island appears to be a source of endemism with one endemic species of *Lipinia* (*L. rouxi*) and the *L. noctua* from that area are also genetically distinct.

Key words: Biogeography; Data-partitions; Likelihood; *Lipinia*; Lygosominae; Minimum Evolution; Multiple datasets; Pacific; Parsimony; Papua

1. Introduction

Lipinia noctua (Reptilia: Scincidae) shows one of the largest distributions of any lizard (Greer, 1974; Adler *et al.* 1995; Austin, 1999). It occurs from the Palau (Belau) archipelago in the north-west and Indonesia in the south-west, through Melanesia into the diverse islands of the Pacific ocean reaching remote Oceania including Hawai'i in the north-east and Easter and Pitcarin Islands in the south-east. *Lipinia noctua*, has been very successful at colonizing islands and occurs on virtually all islands in tropical Oceania including many of the small low-lying atolls. It shows no detectable variation in

morphology across this broad geographic range, and this in combination with the large ocean barriers separating oceanic islands (often hundreds of kilometers), has lead previous researchers to conclude that human-mediated dispersal from New Guinea is the likely mechanism responsible for the current distribution of *Lipinia noctua* (Burt and Burt, 1932: Zweifel, 1979). Molecular work by Austin (1995, 1998, 1999), Bruna *et al.* (1995), Donnellan and Aplin (1989) and morphological work by Greer and Mys (1987) has demonstrated strong morphological conservatism for Pacific scincid lizards despite genetic divergence. Morphological conservatism seems to be especially evident for classical morphological characters such as mid-body scale rows, paravertebral scales, and lamellae under the fourth toe (Austin, 1995).

Recent molecular work on *Lipinia noctua* has shown that the situation for this species is more complex than originally thought. Genetic work by Austin (1999) on *L. noctua* from across its range has shown that most of Micronesia and Melanesia represent natural dispersal while populations east of the Solomon Islands represent recent human-mediated dispersal. Therefore, *L. noctua* is synanthropic for the myriad islands of Oceania, but has shown remarkable natural dispersal abilities in reaching some of the remote islands of Micronesia and Melanesia.

In this paper I address colonization of *Lipinia noctua* in Melanesia by examining genetic variation for a portion of the mitochondrial *cytochrome b* and 12S ribosomal RNA (rRNA) genes. In particular I address questions pertaining to the colonization of New Ireland Island in the Bismarck Archipelago and the degree of genetic divergence within and between populations of *L. noctua*.

2. Materials and methods

2.1. *Specimens, tissue samples, and outgroups*

Tissue samples (muscle and liver) were dissected from freshly sacrificed specimens and either stored at –80 °C or in 70% ethanol. Table 1 lists the species and locality data for all specimens used in this study. Figure 1 shows the *L. noctua* populations sampled.

Previous molecular work on the phylogenetic relationships of *Lipinia* from New Guinea based on allozyme data (Austin, 1995) and DNA sequence variation (Austin, 1998) demonstrates that *Lipinia leptosoma* from Palau is basal to the Papuan *Lipinia* and that the Papuan *Lipinia* may be monophyletic in relation to the *Lipinia* radiation found in the Philippines. *Lipinia leptosoma*, therefore, is used as an outgroup in all phylogenetic

Table 1
Species, museum identification numbers, and localities for specimens used in this study. Numbers in parentheses following species correspond to DNA sequences in Table 2. All acronyms follow Leviton *et al.* (1985).

species	sample size	accession numbers	locality data
Lipinia leptosoma	1	CAS being catalogued	Palau, Babeldaob Is.
Lipinia longiceps	1	TNHC 51284	Papua New Guinea, Madang Province
Lipinia pulchra	1	TNHC51290	Papua New Guinea, Madang Province
Lipinia rouxi	1	TNHC 51436	Papua New Guinea, New Ireland Is.
Lipinia noctua (1, 2)	2	SAMA 4041, 4074	Papua New Guinea, Madang Province
Lipinia noctua (1, 2)	2	TNHC 51481, 51521	Papua New Guinea, Fergusson Is.
Lipinia noctua (1, 2)	2	TNHC 51439, 51440	Papua New Guinea, New Ireland Is., Lelet Platau
Lipinia noctua	1	TNHC 51444	Papua New Guinea, New Ireland Is., Kavieng
Lipinia noctua	1	SAMA B46	Solomon Islands, Mole Is.

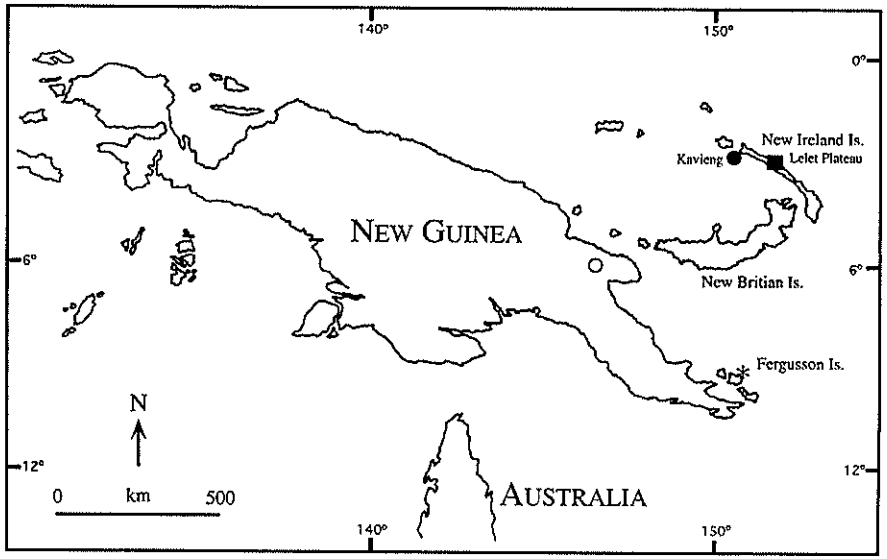

Figure 1. Locality map for *Lipinia noctua* sampled in this study. Open circle: *L. noctua* from north coast New Guinea. Closed circle: *L. noctua* from Kavieng, New Ireland Island. Closed square: *L. noctua* from Lelet Plateau, New Ireland Island. Asterisk: *L. noctua* from Fergusson Island. *Lipinia noctua* population sampled from the Solomon Islands (Mole Island, a small satellite island of Choiseul Island) is not on the map.

analyses and, in addition to the five *L. nocuta* populations sampled, three other *Lipinia* species are included (*L. longiceps, L. pulchra,* and *L. rouxi*).

2.2. *DNA isolation, amplification, and sequencing*

The protocols of Hillis et al. (1990) were followed for the isolation of DNA from both muscle or liver tissue. Approximately 50 mg of either muscle or liver tissue was digested with 20 µl of 10 mg/ml proteinase K for three hours rather than being ground in a mortar and pestle with liquid nitrogen.

Double-stranded DNA products were amplified following the protocols of Palumbi et al. (1991). For the 12S gene two oligonucleotide primers synthesized at the South Australian Museum were used with the polymerase chain reaction (PCR) to amplify and sequence both complementary strands. The 12S primers used were: forward SAM(M1): 5′—TGA CTG CAG AGG GTG ACG GGC GGT GTG T—3′ and reverse SAM(M2): 5′—AAA AAG CTT CAA ACT GGG ATT AGA TAC CCC ACT AT—3′. The *cytochrome b* primers, originally designed by Kocher et al. (1989), were: forward SAM(M5) 5′—AAA AAG CTT CCA TCC AAC ATC TCA GCA TGA TGA AA—3′ and reverse SAM(M6) 5′—AAA CTG CAG CCC CTC AGA ATG ATA TTT GTC CTC A—3′.

Double-stranded PCR products were amplified using a Corbett FTS 320 Thermal cycler. The specific thermal cycle used is as follows: (*i*) one cycle at 94 °C × 3 min, 47 °C × 1 min, and 72 °C × 1 min; (*ii*) thirty four cycles at 94 °C × 45 seconds, 47 °C × 45 seconds, and 72 °C × 1 min; (*iii*) one cycle at 72 °C × 6 min. PCR products were cleaned using BresaClean (Bresatec Ltd.) and then cycle sequenced on Corbett FTS1 Thermal cycler using ABI Prism dye-terminators (ABI) and protocols specified by the manufacturer. Sequences were determined on an ABI 377 DNA automated sequencer.

2.3. *Sequence alignment phylogenetic analysis*

Sequences were aligned using Clustal V (Higgins *et al.*, 1991). Three methods of phylogeny reconstruction were used: maximum parsimony, minimum evolution, and maximum likelihood. The presence of a transition/transversion bias has been well documented with transitions occurring more frequently than transversions (Brown *et al.*, 1982; Vigilant *et al.*, 1989; Knight and Mindell, 1993). Estimation of this transition/transversion bias directly from the data may underestimate the ratio due to multiple substitutions, therefore, maximum likelihood was used to estimate the transition/transversion (TI/TV) ratio (Wakeley, 1996; Purvis and Bromham, 1997).

All phylogenetic analyses were done using PAUP test version 4.0d64, written by D.L. Swofford. The two parameter HKY'85 model was implemented, which uses nucleotide frequencies estimated from the data, for all likelihood analyses (Hasegawa *et al.*, 1985). Heuristic searches with twenty random addition sequences were used to search for shortest trees from possible different local optima. In order to facilitate a reasonable number of bootstrap pseudoreplicates for likelihood, which is computationally expensive, the fast step-wise addition option was implemented. The tree bisection-reconstruction (TBR) branch swapping method was used.

The partition-homogeneity test was used to asses if both genes should be combined in a single analysis. The test examines heterogeneity by calculating the sum of the tree lengths from the original dataset and comparing that with the tree length distribution from pseudopartitions (of original partition size)[Huelsenbeck *et al.*, 1996].

2.4. *Phylogenetic confidence*

Confidence in the phylogenetic signal for this molecular data set was assessed in four ways. First, maximum parsimony, minimum evolution and maximum likelihood were used to estimate a phylogenetic hypothesis (Kim, 1993). Second, maximum parsimony, minimum evolution, and maximum likelihood analyses were bootstrapped to assess confidence for each node (Felsenstein, 1985; Swofford and Olsen, 1990; Hillis and Bull, 1993). Third, presence of a significant phylogenetic signal was assessed using the g_1 statistic estimated from 100,000 random trees (Hillis and Huelsenbeck, 1992). The

Table 2
DNA sequences for 12 samples. Three hundred and thirteen base-pairs for the *Cytochrome b* gene and three hundred and eighty base-pairs for 12S rRNA gene. All sequences are aligned with the outgroup *Lipinia leptosoma*.

	Cytochrome b:
Lipinia leptosoma	GCATGATGAAATTTTGGGTCCCTTCT
Lipinia longiceps	GCATGATGAAACTTCGGCTCTCTACT
Lipinia pulchra	GCATGATGAAACTTTGGTTCCCTTCT
Lipinia rouxi	GCATGATGAAACTTCGGCTCACTCCT
L. noctua New Guinea (1)	GCATGATGAAACTTCGGGTCACTACT
L. noctua New Guinea (2)	GCATGATGAAACTTCGGGTCACTACT
L. noctua Fergusson Is. (1)	GCATGATGAAACTTCGGATCACTACT
L. noctua Fergusson Is. (2)	GCATGATGAAACTTCGGATCACTACT
L. noctua Lelet (1)	GCATGATGAAACTTCGGGTCACTACT
L. noctua Lelet (2)	GCATGATGAAACTTCGGGTCACTACT
L. noctua Kavieng	GCATGATGAAACTTCGGGTCACTACT
L. noctua Solomon Is	GCATGATGAAACTCTGGGTCACTACT

Table 2 (continued)

Lipinia leptosoma	TGGCCTCTGCCTCATTGCACAAGTAATCTCCGGCCTGTTCCTGGCAATAC
Lipinia longiceps	AGGAATATGCCTAATTGTACAAGTACTTACCGGACTATTTTTAGCTATAC
Lipinia pulchra	AGGAGTCTGCTTAATCACACAGGTCCTCACCGGCCTCTTCCTAGCCATAC
Lipinia rouxi	TGGCATGTGCCTAATTGTACAGGTCATCACAGGACTATTTCTAGCCATAC
L. noctua New Guinea (1)	AGGCATATGCCTAGTTGTACAAGTAGCAACTGGACTGTTCCTAGCCATGC
L. noctua New Guinea (2)	AGGCATATGCCTAGTTGTACAAGTAGCAACTGGACTGTTCCTAGCCATGC
L. noctua Fergusson Is. (1)	AGGCATATGCCTGGTTATCCAGGTGGCAACTGGCCTATTCCTAGCCATAC
L. noctua Fergusson Is. (2)	AGGCATATGCCTGGTTATCCAGGTGGCAACTGGCCTATTCCTAGCCATAC
L. noctua Lelet (1)	AGGCATATGCCTAATCGTACAAGTAATAACGGGCCTATTCCTAGCCATAC
L. noctua Lelet (2)	AGGCATATGCCTAATCGTACAAGTAATAACGGGCCTATTCCTAGCCATAC
L. noctua Kavieng	AGGCATATGCCTAATTGTACAAGTAGCAACCGGCCTATTTCTGGCCATGC
L. noctua Solomon Is.	AGGCATATGCCTAATTATCCAAGTAGCAACCGGCCTATTCTTAGCCATGC
Lipinia leptosoma	ACTACACAGCAGATATCTCCTCCGCCTTCTCATCCGTCGCCCACATTTGC
Lipinia longiceps	ACTATACGGCAGACATTTCTTCCGCTTTCTCATCAGTAGCCCATATCTGC
Lipinia pulchra	ATTACACAGCAGACATCTCCTCCGCTTTCTCATCAATCGCCCACATCTGC
Lipinia rouxi	ACTATACAGCAGACATTTCCTCAGCCTTCTCATCTGTGGCCCACATTTGT
L. noctua New Guinea (1)	ACTACACAGCAGACATCTCTTCCGCCTTTTCATCAATTGCTCACATCTCC
L. noctua New Guinea (2)	ACTACACAGCAGACATCTCTTCCGCCTTTTCATCAATTGCTCACATCTCC
L. noctua Fergusson Is. (1)	ACTACACAGCAGACATCTCTTCCGCCTTTTCATCAATTGCTCACATTTGC
L. noctua Fergusson Is. (2)	ACTACACAGCAGACATCTCTTCCGCCTTTTCATCAATTGCTCACATTTGC
L. noctua Lelet (1)	ACTACACAGCAGACATCTCTTCCGCCTTTTCATCAATTGCTCACATCTGC
L. noctua Lelet (2)	ACTACACAGCAGACATCTCTTCCGCCTTTTCATCAATTGCTCACATCTGC
L. noctua Kavieng	ACTACACAGCAGACATCTCTTCCGCCTTTTCATCAATTGCTCACATCTGC
L. noctua Solomon Is.	ACTACACAGCAGACATCTCTTCTGCCTTCTCATCAATCGCCCACATCTGC
Lipinia leptosoma	CGAGACGTTCAATATGGCTGACTAATCCGAAACCTGCACGCCAACGGGGC
Lipinia longiceps	CGAGATGTTCAATACGGCTGACTAATTCGAAACCTCCACGCTAATGGAGC
Lipinia pulchra	CGAGATGTACAATACGGCTGACTAATCCGAAACTTACACGCCAACGGCGC
Lipinia rouxi	CGCGACGTCCAATATGGATGACTAGTCCGCAACCTCCATGCTAACGGCGC
L. noctua New Guinea (1)	CGAGACGTTCAACACGGCTGACTTATCCGCAACCTTCACGCCAACGGCGC
L. noctua New Guinea (2)	CGAGACGTTCAACACGGCTGACTTATCCGCAACCTTCACGCCAACGGCGC
L. noctua Fergusson Is. (1)	CGAGATGTACAACACGGCTGGCTCATCCGCAACCTTCATGCCAACGGCGC
L. noctua Fergusson Is. (2)	CGAGATGTACAACACGGCTGGCTCATCCGCAACCTTCATGCCAACGGCGC
L. noctua Lelet (1)	CGAGACGTTCAACACGGCTGACTCATCCGCAACCTTCATGCCAACGGCGC
L. noctua Lelet (2)	CGAGACGTTCAACACGGCTGACTCATCCGCAACCTTCATGCCAACGGCGC
L. noctua Kavieng	CGAGACGTTCAACACGGCTGATTTATCCGCAACCTTCATGCCAACGGCGC
L. noctua Solomon Is.	CGAGACGTACAATACGGATGACTCATCCGCAACCTTCATGCCAACGGCGC
Lipinia leptosoma	CTCAATATTCTTCATTTGCCTGTTCCTTCATATCGGACGCGGATTATACT
Lipinia longiceps	CTCATTATTTTTCATCTGCCTCTACCTGCACATCGGACGGGGCCTATATT
Lipinia pulchra	CTCTATATTCTTTATCTGCCTGTATCTTCATATCGGACGTGGCTTATACT
Lipinia rouxi	CTCACTATTCTTTATCTGCCTGTACCTCCATATTGGTCGCGGCCTATATT
L. noctua New Guinea (1)	CTCTTTATTCTTCATCTGCTTATATTTGCACATCGGGCGAGGCCTTTACT
L. noctua New Guinea (2)	CTCTTTATTCTTCATCTGCTTATATTTGCACATCGGGCGAGGCCTTTACT
L. noctua Fergusson Is. (1)	CTCTATCTTTTTTATTTGCCTTTACCTGCACATCGGACGAGGCCTTTATT
L. noctua Fergusson Is. (2)	CTCTATCTTTTTTATTTGCCTTTACCTGCACATCGGACGAGGCCTTTATT
L. noctua Lelet (1)	CTCTCTGTTCTTCATCTGCCTATATCTGCACATCGGGCGGGGCCTTTACT
L. noctua Lelet (2)	CTCTCTGTTCTTCATCTGCCTATATCTGCACATCGGGCGGGGCCTTTACT
L. noctua Kavieng	CTCTTTATTCTTCATCTGCTTATATCTGCACATCGGGCGAGGCCTTTACT
L. noctua Solomon Is.	CTCCCTATTCTTTATCTGCTTATACCTTCACATCGGGCGGGGCCTTTATT

Table 2 (continued)

Lipinia leptosoma	ACGGCTCCTACATGTTCAAAGAAACCTGAAACATCGGGGTCGTCCTATTC
Lipinia longiceps	ACGGCTCTTACATATATAAAGAAACATGAAACATCGGAGTAATCTTACTA
Lipinia pulchra	ACGGCTCTTACATATACATAGAGACCTGGAATATTGGAGTCGTATTGCTA
Lipinia rouxi	ATGGCTCATATATATACAAAGAAACATGAAACATTGGCGTCATCCTTCTA
L. noctua New Guinea (1)	ACGGATCATACATGTATAAAGAAACATGAAACATTGGCGTAATACTGCTT
L. noctua New Guinea (2)	ACGGATCATACATGTATAAAGAAACATGAAACATTGGCGTAGTACTGCTT
L. noctua Fergusson Is. (1)	ACGGATCCTACATGTACAAAGAAACATGGAACATTGGTGTAGTGCTGCTA
L. noctua Fergusson Is. (2)	ACGGATCCTACATGTACAAAGAAACATGGAACATTGGTGTAGTGCTGCTA
L. noctua Lelet (1)	ACGGATCCTACCTATACAAAGAAACATGGAACATTGGTGTGGTGCTGCTT
L. noctua Lelet (2)	ACGGGTCCTACCTATACAAAGAAACATGGAACATTGGTGTGGTGCTGCTT
L. noctua Kavieng	ACGGATCCTACATGTACAAAGAAACATGAAACATTGGTGTAGTACTGCTC
L. noctua Solomon Is.	ACGGATCCTACATGTACAAAGAAACATGAAACATTGGTGTCGTGCTATTA
Lipinia leptosoma	CTCCTAGTAATGGCAACAGCTTTCGTTGGCTACGTTC
Lipinia longiceps	CTCCTAGTTATAGCAACAGCCTTCGTAGGCTACGTCC
Lipinia pulchra	CTACTTGTTATAGCAACTGCTTTCGTAGGCTACGTAT
Lipinia rouxi	CTACTAGTAATAGCAACAGCCTTCGTTGGCTATGTCT
L. noctua New Guinea (1)	CTACTAGTGATAGCTACTGCATTTGTAGGGTACGTCC
L. noctua New Guinea (2)	CTACTAGTGATAGCTACTGCATTTGTAGGGTACGTCC
L. noctua Fergusson Is. (1)	CTACTAGTAATAGCAACTGCATTTGTAGGCTATGTCC
L. noctua Fergusson Is. (2)	CTACTAGTAATAGCAACTGCATTTGTAGGCTATGTCC
L. noctua Lelet (1)	CTACTAGTAATAGCAACTGCATTTGTAGGGTACGTCT
L. noctua Lelet (2)	CTACTAGTAATAGCAACTGCATTTGTGGGGTACGTCT
L. noctua Kavieng	CTACTAGTAATAGCAACTGCATTTGTAGGATACGTCC
L. noctua Solomon Is.	CTTCTAGTAATAGCAACTGCATTTGTAGGATATGTCC

12S:

Lipinia leptosoma	CTTAGCCGTAAACAAA
Lipinia longiceps	CTTAACCCTAAACACA
Lipinia pulchra	--------TAAACACA
Lipinia rouxi	--------TAAACACA
L. noctua New Guinea (1)	CTTAGCCTTAAACACA
L. noctua New Guinea (2)	CTTAGCCTTAAACACA
L. noctua Fergusson Is. (1)	CTTAGCCCTAAACACA
L. noctua Fergusson Is. (2)	CTTAGCCCTAAACACA
L. noctua Lelet (1)	CTTAGCCTTAAACACA
L. noctua Lelet (2)	CTTAGCCTTAAACACA
L. noctua Kavieng	CTTAGCCTTAAACACA
L. noctua Solomon Is.	CTCGGCCATAAACACA
Lipinia leptosoma	GATAATACTAACACAACATTATCCGCCAGAGAACTACAAGCGAAAAGCTA
Lipinia longiceps	GATA-TTTTAATACAATACTATCCGCCAGAGAACTACAAGCGAAAAGCTA
Lipinia pulchra	GATA-TTCTAATACACCAATATCCGCCAGAGAACTACAAGCGAAAAGCTA
Lipinia rouxi	GATA-TTCTAACACAATAATATCCGCCAGAGAACTACAAGCGAAAAGCTA
L. noctua New Guinea (1)	GATA-TTTTAATACAATACTATCCGCCAGAGGACTACAAGCGAAAAGCTA
L. noctua New Guinea (2)	GATA-TTTTAATACAATACTATCCGCCAGAGGACTACAAGCGAAAAGCTA
L. noctua Fergusson Is. (1)	GATA-TTTT-GTACACTACTATCCACCAGAGAACTACAAGCGAAAAGCTA
L. noctua Fergusson Is. (2)	GATA-TTTT-GTACACTACTATCCGCCAGAGAACTACAAGCGAAAAGCTA
L. noctua Lelet (1)	GATA-TTTTAATACAATATTATCCGCCAGAGGACTACAAGCGAAAAGCTA
L. noctua Lelet (2)	GATA-TTTTAATACAATATTATCCGCCAGAGGACTACAAGCGAAAAGCTA
L. noctua Kavieng	GATA-TTTTAATACAATATTATCCGCCAGAGGACTACAAGCGAAAAGCTA
L. noctua Solomon Is.	GATA-TTTTAGTACACTA-TATCCGCCAGAGTACTACAAGCGAAAAGCTA

Table 2 (continued)

Lipinia leptosoma	GAAACTCAAAGGACTTGGCGGTGCTTCAAATCAACCTAGAGGAGCCTGTC
Lipinia longiceps	GAAACTCCAAGGACTTGGCGGTGCTTTAAACCAACCTAGAGGAGCCTGTC
Lipinia pulchra	GAAACTCCAAGGACTTGGCGGTGCTTCAAACCAACCTAGAGGAGCCTGTC
Lipinia rouxi	GAAACTCCAAGGACTTGGCGGTGCTTCAAACCAACCTAGAGGAGCCTGTC
L. noctua New Guinea (1)	GAAACTCCAAGGACTTGGCGGTGCTTCAAATCAACCTAGAGGAGCCTGTC
L. noctua New Guinea (2)	GAAACTCCAAGGACTTGGCGGTGCTTCAAATCAACCTAGAGGAGCCTGTC
L. noctua Fergusson Is. (1)	GAAACTCCAAGGACTTGGCGGTGCTTCAAACCAACCTAGAGGAGCCTGTC
L. noctua Fergusson Is. (2)	GAAACTCCAAGGACTTGGCGGTGCTTCAAACCAACCTAGAGGAGCCTGTC
L. noctua Lelet (1)	GAAACTCCAAGGACTTGGCGGTGCTTCAAATCAACCTAGAGGAGCCTGTC
L. noctua Lelet (2)	GAAACTCCAAGGACTTGGCGGTGCTTCAAATCAACCTAGAGGAGCCTGTC
L. noctua Kavieng	GAAACTCCAAGGACTTGGCGGTGCTTCAAATCAACCTAGAGGAGCCTGTC
L. noctua Solomon Is.	GAAACTCCAAGGACTTGGCGGTGCTTCAAACCAACCTAGAGGAGCCTGTC
Lipinia leptosoma	CTATAATCGATAATCCACGATTCACCTTACCACCACTAGCCAACCAGCCT
Lipinia longiceps	CTATAATCGATACTCCACGTTTTACCTTACCCCCGCTAGCCAACCAGCCT
Lipinia pulchra	CTATAATCGATACCCCACGTTCTACCTTACCCCCCTTAGCCC-CCAGCCT
Lipinia rouxi	CTATAATCGATACTCCACGTTAAACCTCACCTCCTTTTGCTAACCAGCCT
L. noctua New Guinea (1)	CTATAATCGATACTCCCCGTTTTACCTCACCTACACTAGTCAACCAGCCT
L. noctua New Guinea (2)	CTATAATCGATACTCCCCGTTTTACCTCACCTACACTAGTCAACCAGCCT
L. noctua Fergusson Is. (1)	CTATAATCGATACCCCACGTTTAACCTCACCCACACTAGCCAATCAGCCT
L. noctua Fergusson Is. (2)	CTATAATCGATACCCCACGTTTAACCTCACCCACACTAGCCAATCAGCCT
L. noctua Lelet (1)	CTATAATCGATATTCCCCGTTTCACCTCACCCACACTAGTCAACCAGCCT
L. noctua Lelet (2)	CTATAATCGATATTCCCCGTTTCACCTCACCCACACTAGTCAACCAGCCT
L. noctua Kavieng	CTATAATCGATACTCCCCGTTTTACCTCACCCACGCTAGTCAGCCAGCCT
L. noctua Solomon Is.	CTATAATCGATACCCCACGTTAAACCTCACCCACACTAGCCAGCCAGCCT
Lipinia leptosoma	ATATACCGCCGTCGCCAGCTCACCCTATGAAAGAAACAAAGTGGGCAAAA
Lipinia longiceps	ATATACCGCCGTCGTCAGCCTACCCTGTGAGAGAAACAAAGTAAGCAAAA
Lipinia pulchra	ATATACCGCCGTCGTCAGCCTACCTTATGAAAGAAACAAAGTAGACAAAA
Lipinia rouxi	ATATACCGCCGTCGTCAGCCTACCTTATGAAAGAAGAAAAGTAGGCAAAA
L. noctua New Guinea (1)	ATATACCGCCGTCGTCAGCTTACCTTATGAAAGAGACAAAGTAAGCAGAA
L. noctua New Guinea (2)	ATATACCGCCGTCGTCAGCTTACCTTATGAAAGAGACAAAGTAAGCAGAA
L. noctua Fergusson Is. (1)	ATATACCGCCGTCGTCAGCTTACCTTATGAAAGAGACAAAGTAAGCAAAA
L. noctua Fergusson Is. (2)	ATATACCGCCGTCGTCAGCTTACCTTATGAAAGAGACAAAGTAAGCAAAA
L. noctua Lelet (1)	ATATACCGCCGTCGTCAGCTTACCTTATGAGAGAAACAAAGTAGGCAAAA
L. noctua Lelet (2)	ATATACCGCCGTCGTCAGCTTACCTTATGAGAGAAACAAAGTAGGCAAAA
L. noctua Kavieng	ATATACCGCCGTCGTCAGCTTACCTTATGAAAGAAATAAAGTAGGCAAAA
L. noctua Solomon Is.	ATATACCGCCGTCGTCAGCCTACCCTATGAAAGAATAAAAGTAGGCAAAA
Lipinia leptosoma	TAGTTA-ACAACTAATACGTCAGGTCAAGGTGTAGCAAACGAG-GTGGTA
Lipinia longiceps	CAACTA-ATAATTAAAACGTCAGGTCAAGGTGTAGCACATGCGGGGG-CA
Lipinia pulchra	CAGTTA-ATAACTAAAACGTCAGGTCAAGGTGTAGCACATGGGGGGGGCA
Lipinia rouxi	TAGTTA-ATAACTAACACGTCAGGTCAAGGTGTAGCACATGGGGAGGA-A
L. noctua New Guinea (1)	TAGTTATACAACTAACACGTCAGGTCAAGGTGTAGCATATGTGTGGGA-A
L. noctua New Guinea (2)	TAGTTATACAACTAACACGTCAGGTCAAGGTGTAGCATATGTGTGGGA-A
L. noctua Fergusson Is. (1)	TAGTTAAACAACTAGTACGTCAGGTCAAGGTGTAGCATATGTGTAGGA-A
L. noctua Fergusson Is. (2)	TAGTTAAACAACTAGTACGTCAGGTCAAGGTGTAGCATATGTGTAGGA-A
L. noctua Lelet (1)	TAGTTATATAACTAACACGTCAGGTCAAGGTGTAGCACATGTGCGGGA-A
L. noctua Lelet (2)	TAGTTATATAACTAACACGTCAGGTCAAGGTGTAGCACATGTGCGGGA-A
L. noctua Kavieng	TAGTTACCTAACTAACACGTCAGGTCAAGGTGTAGCACATGTGTGGGA-A
L. noctua Solomon Is.	TAGTTAAACAACTAACACGTCAGGTCAAGGTGTAGCACATGTGTGGGA-A

Table 2 (continued)

Lipinia leptosoma	GAGATGGGCTACATTTTTACAAAGATAACACACGAACAGTGTGCTGAAAC
Lipinia longiceps	GAGATGGGCTACATTTTCTAAGATG-AACATACAGACAAAATGTTGAAAC
Lipinia pulchra	GAGATGGGCTACATTTTCAA--ACA-AACATACGAATAATGTGTTGAAAC
Lipinia rouxi	GAGATGGGCTACATTTTCAACAATG-AACACACGAATAACATGCTGAAAC
L. noctua New Guinea (1)	GAGATGGGCTACATTTTCAA-AACG-AACATACGAACAATATGTTGAAAC
L. noctua New Guinea (2)	GAGATGGGCTACATTTTCAA-AACG-AACATACGAACAATATGTTGAAAC
L. noctua Fergusson Is. (1)	GAGATGGGCTACATTTTCAA-AACG-AACACACGAACAATATGTTGAAAC
L. noctua Fergusson Is. (2)	GAGATGGGCTACATTTTCAA-AACG-AACACACGAACAATATGTTGAAAC
L. noctua Lelet (1)	GAGATGGGCTACATTTTCAA-AACG-AACACACGAACAATATGTTGAAAC
L. noctua Lelet (2)	GAGATGGGCTACATTTTCAA-AACG-AACACACGAACAATATGTTGAAAC
L. noctua Kavieng	GAGATGGGCTACATTTTCAA-AACG-AACATACGAACGATATGTTGAAAC
L. noctua Solomon Is.	GAGATGGGCTACATTTTCAA-AACG-AACATACGAATAATACGTTGAAAC
Lipinia leptosoma	ACTCACTTGAAGGTGGATTTAGTAGTAAAATGAGTAAGAAAACTTATTTT
Lipinia longiceps	ACATATTAGAAGGTGGATTTAGTAGTAAATTAAGCAAGA-ATACTATTTT
Lipinia pulchra	ACATATTTGAAGGTGGATTTAGTAGTAAAACGACCAAGA-AAAGTATATT
Lipinia rouxi	ACATGTTTAAAGGTGGATTTAGTAGTAAAGAGTATAAGA-AAGACATCTT
L. noctua New Guinea (1)	ACGTATTTAAAGGTGGATTTAGTAGTAAACTAGAAAAGA-AAAACACATT
L. noctua New Guinea (2)	ACGTATTTAAAGGTGGATTTAGTAGTAAACTAGAAAAGA-AAGACACATT
L. noctua Fergusson Is. (1)	ATGTATTTAAAGGTGGATTTAGTAGTAAATTAGAAAAGA-AAAACATCTT
L. noctua Fergusson Is. (2)	ATGTATTTAAAGGTGGATTTAGTAGTAAATTAGAAAAGA-AAAACATCTT
L. noctua Lelet (1)	ACGTATTTAAAGGCGGATTTAGTAGTAAACTAGAAAAGA-AAAACTTCTT
L. noctua Lelet (2)	ACGTATTTAAAGGCGGATTTAGTAGTAAACTAGAAAAGA-AAAACTTCTT
L. noctua Kavieng	ACGTATTTAAAGGCGGATTTAGTAGTAAACTAGAAAAGA-AAAACTTCTT
L. noctua Solomon Is.	ACGTATTTAAAGGTGGATTTAGTAGTAAATTAGAAAAGA-GTACCATCTT
Lipinia leptosoma	-AAACATGCTCTGA
Lipinia longiceps	GAAACCTGCTCTGA
Lipinia pulchra	GAAACCTGCTCTGA
Lipinia rouxi	GAAACCCGCTCTGA
L. noctua New Guinea (1)	GAAACCCGCTCTGA
L. noctua New Guinea (2)	GAAACCCGCTCTGA
L. noctua Fergusson Is. (1)	GAAACCTGCTCTGA
L. noctua Fergusson Is. (2)	GAAACCTGCTCTGA
L. noctua Lelet (1)	GAAACCCGCTCTGA
L. noctua Lelet (2)	GAAACCCGCTCTGA
L. noctua Kavieng	GAAACCCGCTCTGA
L. noctua Solomon Is.	GAAACCCGCTCTGA

g_1 statistic is a measure of the degree of skewness of tree-length distributions, with a large negative g_1 value indicating a large left skew. A significant g_1 indicates the presence of phylogenetic signal.

Fourth, the consistency index (CI), homoplasy index (HI), retention index (RI), and rescaled consistency index (RCI) (Kluge and Farris, 1972; Farris, 1989; Swofford, 1990; Klassen *et al.*, 1991) were calculated using PAUP4.0 to assess the presence of phylogenetic signal.

3. Results

A total of six hundred and ninety three aligned sites, three hundred and thirteen aligned sites for *cytochrome b* and three hundred and eighty aligned sites for 12S, were used in the phylogenetic analysis (Table 2). Of these sites 89, 62 and 151 were informative under the parsimony criterion for the *cytochrome b*, 12S, and combined datasets, respectively. A TI/TV ratio of 2.6, 3.6, and 3.0 was estimated using maximum likelihood from the *cytochrome b*, 12S, and combined datasets, respectively. These TI/TV ratios were used as a weighting scheme in all phylogenetic analyses.

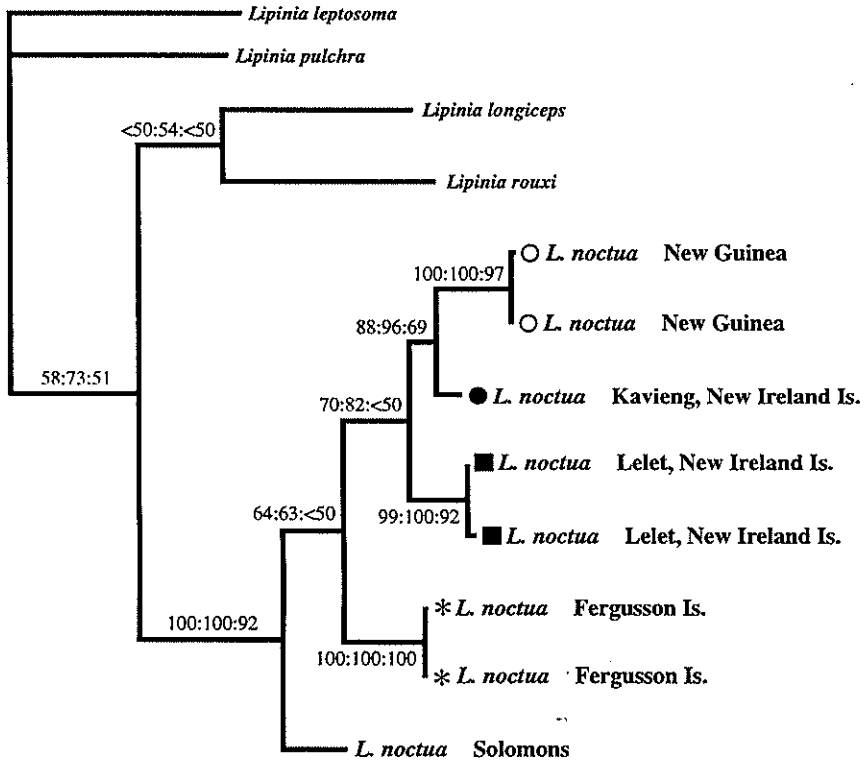

Figure 2. Maximum parsimony phylogram for eight populations of *Lipinia noctua* and four species of *Lipinia* from *cytochrome b*. *Lipinia leptosoma* from Palau is the outgroup taxa (Austin, 1998). Numbers at nodes correspond to 100 bootstrap pseudoreplicates for maximum parsimony, minimum evolution and maximum likelihood, respectively. Symbols are the same as those in Figure 1.

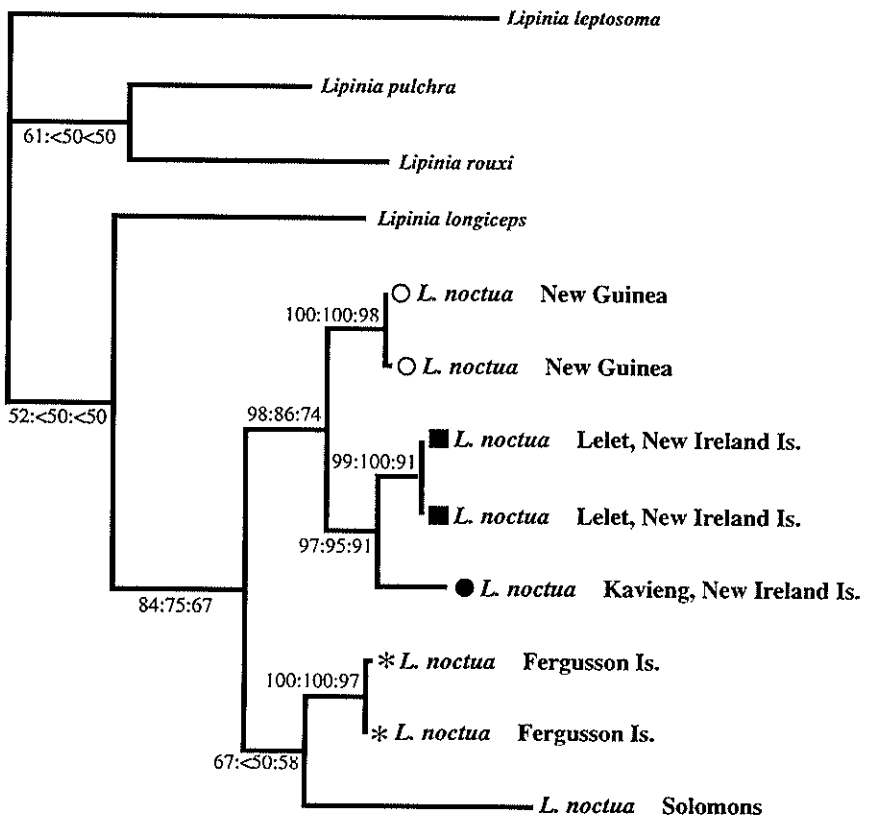

Figure 3. Maximum parsimony phylogram for eight populations of *Lipinia noctua* and four species of *Lipinia* from 12S. Numbers at nodes correspond to 100 bootstrap pseudoreplicates for maximum parsimony, minimum evolution and maximum likelihood, respectively. Symbols are the same as those in Figure 1.

No insertion/deletion (indels) events are present in the alignment for *cytochrome b*, but several are present within the aligned 12S sequences. *Cytochrome b* is a protein-encoding gene and an open reading frame was observed for all taxa. As the ribosomal 12S gene is not a protein-encoding gene, indels need not be in multiples of three nucleotides.

The partition homogeneity test for the unweighted datasets was significant ($P = 0.02$), indicating the *cytochrome b* and 12S datasets should not be combined given no TI/TV

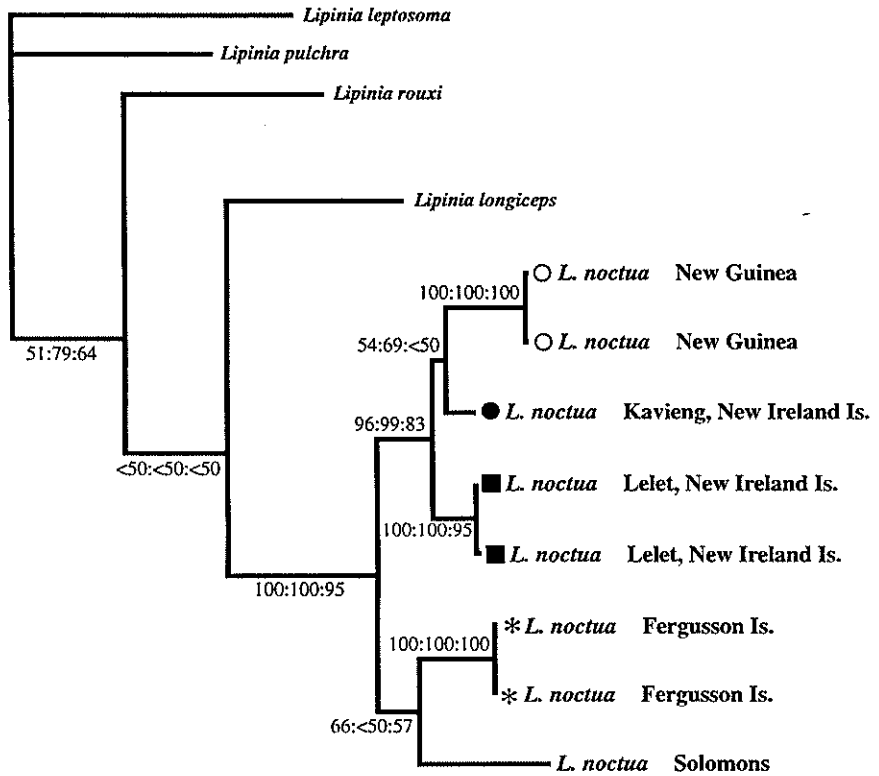

Figure 4. Maximum parsimony phylogram for eight populations of *Lipinia nocuta* and four species of *Lipinia* from the combined *cytochrome b* and 12S datasets. Numbers at nodes correspond to 100 bootstrap pseudoreplicates for maximum parsimony, minimum evolution and maximum likelihood, respectively. Symbols are the same as those in Figure 1.

weighting. The partition homogeneity test, however, for the weighted (TI/TV = 3.0) was non-significant ($P = 0.41$), indicating an appropriate weighting scheme resolves to some degree the conflict between the data partitions and therefore, the two datasets should be combined. Clearly, some heterogeneity exits between both datasets, but this appears to be a result in the more quickly evolving transitions. The down-weighting of transitions seems to reduce conflict. When only transversions are examined the P value for the partition homogeneity test increases ($P = 0.62$).

Because of the results from the partition homogeneity test, both separate and

combined analyses are presented. The single maximum parsimony (MP) tree for the *cytochrome b* dataset is presented in Figure 2. The single MP tree for the 12S dataset is presented in Figure 3. The single MP tree for the combined datasets is presented in Figure 4. Bootstrap support for each node is presented for the three phylogenetic reconstruction methods. Bootstrap proportions in Figures 2–4 are for 100 pseudoreplicates for all analyses.

For the combined analysis (Figure 4) There is strong bootstrap support for the

Table 3
Summary of genetic distance values for *Cytochrome b* only. Uncorrected genetic distances below the diagonal, HKY'85 corrected distances above the diagonal (Hasegawa *et al.*, 1985).

	1	2	3	4	5	6
1 *Lipinia leptosoma*	—	0.24318	0.21083	0.23287	0.27741	0.27251
2 *Lipinia longiceps*	0.20447	—	0.23114	0.20273	0.21615	0.22071
3 *Lipinia pulchra*	0.18211	0.19489	—	0.2558	0.25960	0.25480
4 *Lipinia rouxi*	0.19808	0.17572	0.21406	—	0.26154	0.26645
5 *L. noctua* New Guinea (1)	0.23003	0.18530	0.21725	0.21725	—	0.00321
6 *L. noctua* New Guinea (2)	0.22684	0.18850	0.21406	0.22045	0.00319	—
7 *L. noctua* Fergusson Is. (1)	0.23003	0.20128	0.19808	0.20447	0.12141	0.11821
8 *L. noctua* Fergusson Is. (2)	0.23003	0.20128	0.19808	0.20447	0.12141	0.11821
9 *L. noctua* Lelet (1)	0.21406	0.18850	0.18530	0.19489	0.08946	0.08626
10 *L. noctua* Lelet (2)	0.21406	0.19169	0.18850	0.19489	0.09585	0.09265
11 *L. noctua* Kavieng	0.20447	0.18211	0.20447	0.20767	0.05751	0.05431
12 *L. noctua* Solomon Is.	0.20447	0.19169	0.20128	0.19169	0.13099	0.12780

	7	8	9	10	11	12
1 *Lipinia leptosoma*	0.27779	0.27779	0.25405	0.25402	0.24069	0.24044
2 *Lipinia longiceps*	0.24000	0.24000	0.22066	0.22523	0.21245	0.22499
3 *Lipinia pulchra*	0.23326	0.23326	0.21412	0.21853	0.24227	0.23803
4 *Lipinia rouxi*	0.24108	0.24108	0.22822	0.22819	0.24703	0.22411
5 *L. noctua* New Guinea (1)	0.13479	0.13479	0.09691	0.10458	0.06044	0.14714
6 *L. noctua* New Guinea (2)	0.13075	0.13075	0.09310	0.10072	0.05689	0.14299
7 *L. noctua* Fergusson Is. (1)	—	0.00000	0.11154	0.11937	0.11212	0.12371
8 *L. noctua* Fergusson Is. (2)	0.00000	—	0.11154	0.11937	0.11212	0.12371
9 *L. noctua* Lelet (1)	0.10224	0.10224	—	0.00643	0.07167	0.12338
10 *L. noctua* Lelet (2)	0.10863	0.10863	0.00639	—	0.07906	0.13139
11 *L. noctua* Kavieng	0.10224	0.10224	0.06709	0.07348	—	0.10436
12 *L. noctua* Solomon Is.	0.11182	0.11182	0.11182	0.11821	0.09585	—

Table 4
Summary of genetic distance values for 12S rRNA only. Uncorrected genetic distances below the diagonal, HKY'85 corrected distances above the diagonal (Hasegawa *et al.*, 1985).

	1	2	3	4	5	6
1 *Lipinia leptosoma*	—	0.17741	0.14299	0.17082	0.16415	0.16416
2 *Lipinia longiceps*	0.15510	—	0.10387	0.15056	0.13501	0.13844
3 *Lipinia pulchra*	0.12903	0.09604	—	0.11123	0.13199	0.13542
4 *Lipinia rouxi*	0.15076	0.13415	0.10179	—	0.12040	0.11710
5 *L. noctua* New Guinea (1)	0.14526	0.12067	0.11865	0.10996	—	0.00267
6 *L. noctua* New Guinea (2)	0.14529	0.12334	0.12135	0.10728	0.00267	—
7 *L. noctua* Fergusson Is. (1)	0.14782	0.12078	0.11566	0.10982	0.06141	0.06408
8 *L. noctua* Fergusson Is. (2)	0.14517	0.11809	0.11293	0.10712	0.05875	0.06141
9 *L. noctua* Lelet (1)	0.13711	0.12064	0.11870	0.10179	0.04267	0.04533
10 *L. noctua* Lelet (2)	0.13711	0.12064	0.11870	0.10179	0.04267	0.04533
11 *L. noctua* Kavieng	0.15326	0.12334	0.11591	0.10711	0.04533	0.04800
12 *L. noctua* Solomon Is.	0.16449	0.12341	0.10468	0.09589	0.08283	0.08550

	7	8	9	10	11	12
1 *Lipinia leptosoma*	0.16764	0.16407	0.15344	0.15344	0.17445	0.18923
2 *Lipinia longiceps*	0.13522	0.13174	0.13494	0.13494	0.13804	0.13758
3 *Lipinia pulchra*	0.12826	0.12479	0.13147	0.13147	0.12767	0.11359
4 *Lipinia rouxi*	0.12071	0.11736	0.11043	0.11043	0.11668	0.10354
5 *L. noctua* New Guinea (1)	0.06494	0.06192	0.04447	0.04447	0.04727	0.08849
6 *L. noctua* New Guinea (2)	0.06796	0.06493	0.04739	0.04739	0.05020	0.09159
7 *L. noctua* Fergusson Is. (1)	—	0.00268	0.08026	0.08026	0.08946	0.07390
8 *L. noctua* Fergusson Is. (2)	0.00267	—	0.07715	0.07715	0.0862	0.07085
9 *L. noctua* Lelet (1)	0.07475	0.07208	—	0.00000	0.03020	0.08876
10 *L. noctua* Lelet (2)	0.07475	0.07208	0.00000	—	0.03020	0.08876
11 *L. noctua* Kavieng	0.08275	0.08008	0.02933	0.02933	—	0.08247
12 *L. noctua* Solomon Is.	0.06956	0.06690	0.08307	0.08307	0.07773	—

monophyly of populations (where more than one individual was sampled). For interpopulation relationships, there is a low level of support for the Kavieng population grouping with the north coast New Guinea population. There is also low level of support for a clade consisting of Fergusson Island and Solomon Islands. There is strong support, however, for the monophyly of the New Guinea, Kavieng and Lelet populations.

The main differences between the phylogenetic hypothesis based on *cytochrome b*

Table 5
Summary of genetic distance values for combined *Cytochrome b* and 12S rRNA genes. Uncorrected genetic distances below the diagonal, HKY'85 corrected distances above the diagonal (Hasegawa *et al.*, 1985).

	1	2	3	4	5	6
1 *Lipinia leptosoma*	—	0.20613	0.17332	0.19829	0.21342	0.21137
2 *Lipinia longiceps*	0.17737	—	0.15965	0.17417	0.17083	0.17473
3 *Lipinia pulchra*	0.15349	0.14180	—	0.17454	0.18810	0.18806
4 *Lipinia rouxi*	0.17237	0.15340	0.15376	—	0.18180	0.18178
5 *L. noctua* New Guinea (1)	0.18383	0.15013	0.16413	0.15935	—	0.00292
6 *L. noctua* New Guinea (2)	0.18240	0.15305	0.16412	0.15935	0.00291	—
7 *L. noctua* Fergusson Is. (1)	0.18545	0.15760	0.15394	0.15354	0.08877	0.08877
8 *L. noctua* Fergusson Is. (2)	0.18400	0.15614	0.15246	0.15208	0.08732	0.08731
9 *L. noctua* Lelet (1)	0.17216	0.15156	0.14932	0.14457	0.06395	0.06395
10 *L. noctua* Lelet (2)	0.17218	0.15301	0.15077	0.14457	0.06686	0.06686
11 *L. noctua* Kavieng	0.17653	0.15020	0.15674	0.15346	0.05087	0.05087
12 *L. noctua* Solomon Is.	0.18264	0.15467	0.14941	0.14020	0.10480	0.10480

	7	8	9	10	11	12
1 *Lipinia leptosoma*	0.21586	0.21380	0.19746	0.19747	0.20363	0.21173
2 *Lipinia longiceps*	0.18117	0.17915	0.17271	0.17464	0.17106	0.17624
3 *Lipinia pulchra*	0.17509	0.17310	0.16821	0.17011	0.17821	0.16836
4 *Lipinia rouxi*	0.17386	0.17190	0.16215	0.16215	0.17372	0.15675
5 *L. noctua* New Guinea (1)	0.09588	0.09415	0.06779	0.07110	0.05322	0.11442
6 *L. noctua* New Guinea (2)	0.09586	0.09413	0.06778	0.07109	0.05321	0.11441
7 *L. noctua* Fergusson Is. (1)	—	0.00146	0.09433	0.09779	0.09968	0.09612
8 *L. noctua* Fergusson Is. (2)	0.00146	—	0.09260	0.09605	0.09793	0.09438
9 *L. noctua* Lelet (1)	0.08730	0.08585	—	0.00292	0.04867	0.10413
10 *L. noctua* Lelet (2)	0.09021	0.08875	0.00291	—	0.05187	0.10762
11 *L. noctua* Kavieng	0.09167	0.09022	0.04651	0.04942	—	0.09217
12 *L. noctua* Solomon Is.	0.08888	0.08743	0.09613	0.09903	0.08595	—

and the phylogenetic hypothesis based on 12S is the placement of the Kavieng population. For the *cytochrome b* dataset the Kavieng population groups with the New Guinea population with moderate level of bootstrap support (88: 96: 69) while the Kavieng population groups with the Lelet population for the 12S data set with high levels of bootstrap support (97: 95: 91). In the combined analysis, the Kavieng population groups

with the New Guinea population, as for *cytochrome b*, but with an even lower level of support (54: 69: <50).

The g_1 (estimated from 100,000 randomly generated trees) was –0.85 ($P < 0.01$), –0.79 ($P < 0.01$), and –0.84 ($P < 0.01$) indicating significant phylogenetic signal for *cytochrome b*, 12S, and the combined data, respectively (Hillis and Huelsenbeck, 1992).

Scores for the MP analyses for the three analyses were tree length = 386, 325.4, 723; CI = 0.67, 0.77, 0.70; HI = 0.33, 0.23, 0.30; RI = 0.64, 0.68, 0.64; and RCI = 0.43, 0.52, 0.45 for the *cytochrome b*, 12S, and combined datasets, respectively. Fractional tree lengths are the result of a non-integer estimate of the TI/TV.

The matrix for both uncorrected and HKY'85 corrected genetic distances, is presented in Table 3 for *cytochrome b*, Table 4 for 12S and the combined datasets in Table 5. Comparison of Table 3 with Table 4 shows that *cytochrome b* has a faster rate of evolution compared with 12S. Levels of sequence divergence between populations for *L. noctua* ranged from 2.9% (between the Lelet and Kavieng populations for 12S) to 13% (between the New Guinea and Solomon Islands populations for *cytochrome b*). Within population genetic divergence is low, ranging from 0% (Lelet, 12S; Fergusson Is., *cytochrome b*) to 0.64% (Lelet, *cytochrome b*).

4. Discussion

The ability of animals to colonize islands has intrigued biologists for centuries. The mechanism of over-water dispersal by rafting on vegetation has always been assumed as the most likely means for island colonization. Long over-water dispersal events have been hypothesized to explain a variety of unusual distribution patterns. One enigmatic biogeographic distribution in the Pacific is the Iguanid genus *Brachylophus* endemic to the Tongan and Fijian archipelagos (Cogger, 1974; Gibbons, 1981, 1985). *Brachylophus* is an iguanine iguanian, with its closest relatives being from the Americas. Several authors have argued that long distance over-water dispersal from the Americas is responsible for the distribution of *Brachylophus* in the Pacific. Direct observation of such rare events have made the study of this mode of dispersal difficult. Recently, however, one such rafting event and the establishment and subsequent reproduction of a population has been documented for another Iguanid, *Iguana iguana*, in the West Indies demonstrating that such events, even for relatively large animals, are feasible (Censky *et al.*, 1998).

Although the rafting event for *Iguana iguana* was mediated by a hurricane, similar

Table 6
Thirty species of scincid lizards currently known from the Bismarck Archipelago. Species are identified by 'type,' as either Continental type occurring on the main island of New Guinea as well as the Bismarcks, or Pacific type occurring on multiple archipelagos in the Pacific including the Bismarcks (but excluding New Guinea), or Endemic type meaning they are only found in the Bismarck archipelago.

SPECIES	TYPE
Carlia fusca	Continental
Cryptoblepharus sp.	Continental/Endemic?
Emoia cyanura	Pacific
Emoia impar	Pacific
Emoia atrocostata	Continental
Emoia bismarckensis	Endemic
Emoia caeruleocauda	Continental
Emoia cyanogaster	Pacific
Emoia jakati	Continental
Emoia kordoana	Continental
Emoia longicauda	Continental
Emoia mivarti	Endemic
Emoia nigra	Pacific
Emoia pallidiceps	Continental
Eugongylus albofasiolatus	Continental
Eugongylus rufescens	Continental
Geomyersia coggeri	Endemic
Lamprolepis smaragdina	Continental
Lipinia noctua	Continental/Endemic
Lipinia rouxi	Endemic
Sphenomorphus derooijae	Continental
Sphenomorphus jobiensis	Continental
Sphenomorphus neuhaussi	Continental
Sphenomorphus pratti	Continental
Sphenomorphus solomonis	Continental
Sphenomorphus stickeli	Continental
Sphenomorphus tanneri	Pacific
Tiliqua gigas	Continental
Tribolonotus annectens	Endemic
Tribolonotus brongersmai	Endemic

mechanisms of storm driven rafting/colonization events are possibly responsible for the colonization of the many islands of the Bismarck archipelago. In addition, the large Sepik river draining the highlands of New Guinea flows north into the Bismarck sea

and this may also be an avenue for dispersal. As flood waters rise during the wet season, large trees and mats of vegetation may be swept down the river and ejected into the Bismarck sea. Given appropriate currents and/or winds these riverine rafts may be at least partly responsible for the large herpetological diversity of the Bismarck Archipelago.

The diversity of skinks in the Bismarck archipelago is large with 30 described species (Table 6). Of these, at least six are endemic to the Bismarck archipelago. The speciose genus *Emoia* is represented by 12 species of which two are endemic (Mys, 1988; Brown, 1991). Therefore, this archipelago has clearly been colonized independently from scincid lingeages from mainland New Guinea many times. Given the data presented in this paper, it also appears that the *Lipinia nocuta* from the Lelet Plateau are also genetically distinct from the New Guinea mainland populations (and the lowland New Ireland Kavieng population) and may represent an endemic form. Based on a very rough estimate of time since divergence of 2% per million years (Thorpe *et al.*, 1994) this suggests the Lelet population has been isolated for approximately two to four million years. At present it is unclear if the Kavieng population represents a secondary invasion from the New Guinea mainland or represents genetic divergence of highland and lowland populations on New Ireland Island from a single colonization event. Further population genetic work on *L. nocuta* should clarify this issue. The islands of the Bismarck archipelago have not been adequately surveyed for herpetological diversity. Further survey efforts combined with morphological and molecular genetic work may therefore, demonstrate that the number of endemic species is much greater than currently supposed.

There is a close phylogenetic relationship between the Fergusson Island population and the Solomon Islands population, suggesting that colonization of the Solomon Islands was from the D'entrecasteaux islands rather than from the northern route from the Bismarcks to Bougainville and into the Solomons. The northern route has been widely viewed as the most likely faunal pathway from New Guinea to the Solomons. However, the southern pathway is also observed in molecular phylogeographic data for the Pacific island boa, *Candoia carinata* (Austin, unpublished data), and thus may represent a common faunal dispersal route.

Further population sampling of *L. noctua* within the Bismarck Archipelago will be very important for understanding the degree of population structure for this species. An understanding of the evolutionary history of this widespread species may identify larger patterns of herpetofaunal diversity allowing biologists to identify areas of endemism and genetic diversity. These data are critical for identifying areas to protect in a region of the world under heavy environmental pressure (at present mainly due to logging).

The Bismarck Archipelago appears to be the source area from which all populations of *L. noctua* in the central and eastern Pacific were derived (Austin, 1999). Further sampling within the Bismarck Archipelago to identify the source population may provide insight into the early stages of the human movements into the Pacific by identifying areas to direct archeological research. At present our understanding of the herpetofaunal diversity and distribution for New Guinea and the Bismarcks is poorly known and only by further sampling and biogeographic and phylogenetic analyses will we be able to fully understand faunal and biogeographic patterns for this complex region.

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